

## CORAL–SEAWEED–GRAZER–NUTRIENT INTERACTIONS ON TEMPERATE REEFS<sup>1</sup>

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**Abstract.** Why corals dominate tropical reefs but are rare or absent on temperate reefs is one of the more intriguing global-scale questions in marine ecology. Restriction of corals from temperate reefs has been suggested to be due to low temperature, competition with seaweeds, and synergistic interactions of physical and biological factors. However, most studies addressing these hypotheses have been non-experimental and conducted on tropical corals and reefs near the extremes of their distribution rather than in temperate habitats using corals that are physiologically suited to temperate environments. Some corals occur only in temperate regions, but their ecology is largely unstudied. In an attempt to understand how temperate corals function at latitudes where corals are relatively rare and where reefs tend to be dominated by seaweeds, we examined responses of the temperate coral *Oculina arbuscula* to competition with seaweeds on reefs in North Carolina (USA). We asked how competitive interactions were affected by levels of grazing, nutrients, or interactions of these factors.

Sampling of 12 reef habitats ranging from 1 m deep, inshore sites to 25 m deep, offshore sites demonstrated a strong negative relationship between percentage cover of seaweeds and density of *Oculina* colonies. Seaweeds dominated well-lit habitats (shallow inshore reefs or deep offshore reefs with clear waters), while coral was significantly more abundant in low-light habitats where seaweeds were rare (deep inshore habitats or nearshore reefs with turbid waters). This general among-site pattern also occurred within an individual site as one moved from shallow, well-lit waters to deeper, darker waters. Corals transplanted into seaweed-dominated areas grew well if seaweed canopies were removed but grew poorly, or not at all, if canopies were left intact.

Seaweeds also significantly inhibited recruitment of *O. arbuscula*. At a turbid inshore reef, recruitment was high at a depth of 6 m where seaweeds were rare, but very low at a depth of 1 m where seaweeds were abundant. Removal of seaweeds from shallow plots increased recruitment about 12-fold to levels that did not differ significantly from those at 6 m. In grazer-exclusion cages on offshore reefs, *Oculina* recruitment varied significantly between sites and years. Almost no recruitment was observed at a well-lit, plant-dominated site while recruitment was higher, to very high, at a turbid site with few seaweeds. At this turbid site, recruitment was facilitated by grazing but could not be related to grazer effects on seaweeds. Facilitation was apparently due to consumers removing barnacles, which dominated this low-light site if grazers were excluded.

Cage exclusion of larger herbivores at two offshore sites (primarily fishes) and one inshore site (fishes and urchins) had no significant effect on coral growth. At the well-lit inshore site, herbivores had a large effect on the species composition of the seaweed community, but little effect on the total abundance of seaweeds. Large grazers caused palatable red seaweeds to be replaced by similar amounts of unpalatable brown seaweeds. Therefore, herbivory alone had little impact on total seaweed abundance and the levels of seaweed competition affecting co-occurring *O. arbuscula*. In contrast, when we conducted a factorial experiment manipulating both herbivory and nutrient levels, exclusion cages significantly reduced coral growth. In this experiment, nutrient addition had no effect on brown seaweeds but significantly increased the percentage cover of red seaweeds in exclusion cages. Nutrient addition also tended to suppress coral growth in herbivore-exclusion cages where red seaweeds were stimulated, but to increase coral growth in open cages where herbivores had removed the red seaweeds. Thus, nutrients and herbivory may have acted synergistically to affect seaweeds, and hence corals, on this temperate reef. Different groups of algae (red vs. brown) experienced differential degrees of nutrient limitation and exerted differential competitive effects on corals at this site. Our findings show that competition with seaweeds plays a large role in excluding *Oculina* from well-lit temperate reefs, and support the hypothesis that seaweed competition may interact with latitudinal changes in physical parameters to limit coral recruitment, growth, and accumulation at high latitudes, thus suppressing the potential for reef development.

**Key words:** competition; coral recruitment; coral–seaweed interactions; field experiment; grazers on coral and seaweed; North Carolina (USA) reefs; nutrients and grazers, interactive effects of; *Oculina arbuscula*; reefs, temperate vs. tropical; seaweeds; temperate coral, ecology of.

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## INTRODUCTION

One of the most striking patterns in biogeography is the dominance of corals on tropical reefs, the dominance of seaweeds on temperate reefs, and the largely non-overlapping distribution of these community types where they meet at temperate-tropical boundaries. The ecology of each of these communities is relatively well studied within those geographic regions where they usually occur. There have been, however, few attempts to experimentally determine why corals, and the reefs they are capable of forming, are so poorly represented in temperate locations.

There are hundreds of studies addressing the ecology, physiology, evolution, and natural history of tropical coral reefs (see Choat et al. [1988] and Jackson [1991] for an introduction to this literature). Because scleractinian corals form the physical framework and topographic complexity upon which these reef communities are built, an impressively large number of investigations have focused on the basic biology of these corals and on the physical parameters and biological interactions affecting their ecology and evolution (see reviews by Darwin 1842, Connell 1973, Birkeland 1988, Glynn 1988a, Jackson 1991).

In contrast to tropical reefs, corals are rare on temperate reefs where biogenic complexity is provided primarily by large seaweeds (Schiel and Foster 1986). Corals do occur in shallow temperate habitats but, in contrast to the massive formations of tropical corals, they are most often small solitary organisms (e.g., *Balanophyllia elegans*, 30°–50° N in the eastern Pacific; *Caryophyllia smithii*, 40°–50° N in the eastern North Atlantic) or, if colonial, diminutive in size (e.g., *Astrangia danae*, <5 cm in diameter, ranging from 32° to 45° N in the western Atlantic) and do not form accreting reef structures. *Balanophyllia* and *Astrangia* are probably the most studied shallow, temperate coral genera, but almost all investigations have focused on coral and/or symbiont physiology or on reproduction and larval dispersal (e.g., Szmant-Froelich et al. 1980, Gerrodette 1981, Fadlallah 1982, 1983, Jacques et al. 1983, Szmant-Froelich and Pilon 1984, Coyer et al. 1993). Only one investigation focused on some of the basic biological interactions (Coyer et al. 1993) that are so often investigated for tropical corals (Lang 1973, Potts 1977, Wellington 1982, Birkeland 1988, Glynn 1988a).

Cold temperature at high latitudes is the classical explanation for the lack of scleractinian abundance, vigor, and reef formation in temperate habitats (Dana 1843); however, because many temperate, or even subarctic, habitats around the world support some coral species (Squires and Keyes 1967, Jacques et al. 1983, Schuhmacher and Zibrowius 1985, Ruppert and Fox 1988), temperature alone is not an insurmountable physiological constraint. It is thus unlikely that tem-

perature alone adequately explains: (1) why radiation of corals from tropical to temperate habitats has occurred so rarely, (2) why temperate corals don't accrete reefs, or (3) why hard substrates at low latitudes often support coral reefs while those at higher latitudes usually support seaweed beds. Johannes et al. (1983) suggested that latitudinal variation in physical factors (including, but not limited to, temperature) affect corals indirectly by altering biotic interactions, shifting competitive advantage to seaweeds at higher latitudes, and thereby restricting corals and reef formation to the tropics. This hypothesis was based on observations of tropical reef corals growing at marginally tropical latitudes in Western Australia. However, the effects of seaweed competition on corals that are native to temperate regions, and the effects of environmental factors such as grazing and nutrient levels on coral-seaweed competition in temperate systems have not been rigorously examined.

Conceptual models suggest that low nutrients (Birkeland 1988) interacting with intense grazing (Littler and Littler 1984) aid in maintaining the dominance of corals in the tropics, and several experimental investigations on tropical reefs directly demonstrate the importance of herbivores (Birkeland 1977, Potts 1977, Lewis 1986, Hughes et al. 1987, Hughes 1989) or strongly suggest the importance of low nutrients (Smith et al. 1981, Tomascik and Sander 1987, Littler et al. 1991) in maintaining the abundance of corals on tropical reefs. Additionally, it now seems generally accepted that herbivory decreases and nutrient availability apparently increases with increasing latitude in both terrestrial and marine communities (Birkeland and Randall 1981, Gaines and Lubchenco 1982, Hatcher and Rimmer 1985, Horn 1989, Coley and Aide 1991). If decreased herbivory and increased nutrients favor seaweeds over corals, then these geographic patterns would fit well with the hypothesis of Johannes et al. (1983) about how alterations in coral-seaweed interactions limit coral abundance at higher latitudes (also see Littler and Littler 1984).

The traditional approach to addressing questions of coral and reef biogeography has been to examine factors limiting the growth of tropical reef-building corals at the latitudinal limits of their distribution (Johannes et al. 1983, Hatcher 1985, Crossland 1988). Though limited in number, investigations using this approach have yielded considerable insight, but this approach also has important limitations. It is not unreasonable to assume that most successful tropical corals would not do well under temperate conditions of increased turbidity and nutrients, lowered temperatures and light levels, potentially greater competitive pressures from seaweeds, or several other physical or biological regimes that may vary between temperate and tropical systems. Thus, if tropical corals experience low fitness at their geographic limits due to habitat characteristics

that are rare throughout much of their distribution, is it reasonable to assume that temperate corals, which are presumably better adapted to these habitats, would experience the same difficulties? We think not. As an example, tropical corals are severely affected by low temperatures and sedimentation (Jokiel and Coles 1977, Rogers 1990), yet the temperate coral we investigated appeared to be very tolerant of both of these potential stresses, as evidenced by its high abundance at turbid, cold sites.

Rather than investigating a tropical coral at its geographic extreme, we chose to investigate the temperate coral (*Oculina arbuscula*) that is the most abundant, most widely distributed locally (i.e., inshore to off-shore, shallow to deep, etc.), and thus presumably most successful of the local temperate species. This coral, as well as most tropical corals, is not a true reef builder; however, we wanted to start documenting some of the reasons why *Oculina*, like many other species, cannot accumulate at rates that allow reef-like structures to develop. We reasoned that studying a temperate species to understand why reefs don't accumulate in temperate systems was as valid as the previous studies focused on tropical corals at their distributional extremes. Additionally, we felt that using this different approach was more likely to produce data that might provide novel insights into this larger-scale question. We don't contend that the approach used by previous investigators is flawed and ours superior, but we do contend that this broad question will be more thoroughly and more powerfully addressed if data from both approaches (and possibly others) are available.

In this study, though we are addressing only a single temperate species in one geographical region, we begin to document experimentally some of the ecological factors, or groups of interacting factors, that restrict this coral's growth, distribution, and abundance and may thus prevent it from accumulating at rates that would allow reef formation. Using field observations and manipulative experiments, we specifically addressed the following questions: (1) Do distribution patterns for *Oculina arbuscula* and seaweeds suggest that seaweeds may be competitively displacing the coral? (2) Do seaweeds inhibit the growth and recruitment of *O. arbuscula* on reefs in North Carolina? (3) How do large grazers affect coral growth, coral recruitment, and seaweed abundance and species composition? (4) How does nutrient addition or the interaction of nutrient addition with grazing affect coral growth, seaweed abundance, and seaweed species composition?

#### METHODS

##### *Organisms and sites*

*Oculina arbuscula* is a scleractinian coral endemic to nearshore hard-bottom habitats in North and South Carolina, USA (Ruppert and Fox 1988). Branching colonies can reach 50 cm in diameter, but in less favorable

habitats an encrusting morphology is more common. *O. arbuscula*, like many temperate scleractinia (Schuhmacher and Zibrowius 1985), seems only facultatively associated with endosymbiotic zooxanthellae. Colonies in well-lit habitats are brown due to high densities of endosymbiotic zooxanthellae containing abundant photopigments, while those in dark habitats are white, indicating low levels of photopigments (Miller 1995).

We conducted field experiments at three sites—an inshore rock jetty at Radio Island North Carolina, USA (34°42' N, 76°41' W) and two natural rocky reefs that we termed the 8-km and 43-km reefs in Onslow Bay, North Carolina USA (coordinates given in Table 1). Radio Island Jetty, like many jetties in the South Atlantic Bight, supports a lush and diverse assemblage of seaweeds and sessile benthic invertebrates including both temperate and tropical species (Hay and Sutherland 1988). Abundant grazers are omnivorous and include the spottail pinfish *Diplodus holbrooki*, the pinfish *Lagodon rhomboides*, and the sheepshead *Archosargus probatocephalus*, all of which are abundant in summer. The purple sea urchin *Arbacia punctulata* is common year-round. Water is turbid (visibility often  $\approx 1$  m), seasonal temperatures fluctuate from 5° to 28°C (monthly maximum and minimum readings from August 1991 to March 1992), and tidal currents are strong. *Oculina arbuscula* is common. Inorganic nitrogen concentrations in North Carolina inshore waters are variable, ranging from 0 to 6  $\mu\text{mol/L}$  (Litaker et al. 1987).

The 8-km reef site ( $\approx 8$  km offshore) consists of a rock ledge at a depth of 15 m that drops precipitously to a sandy bottom at 18 m. The ledge margin is dominated by *Oculina arbuscula* with a sparse seaweed cover (estimated at  $<10\%$ ; M. W. Miller and M. E. Hay, *personal observation*) on the sand veneer above the ledge. Water is fairly turbid, with visibility often  $<3$  m. Farther offshore, in clearer oceanic waters, the 43-km reef is a similar ledge with its top at 27 m and its base at 30 m depth. Turbidity here is low, and visibility at this site often exceeds 20 m. *O. arbuscula* is extremely rare at this site, and a bed of brown algae (primarily *Sargassum*, *Dictyopteris*, *Zonaria*, and *Dictyota*) with high cover (often 70–100%) and biomass occupies the area above the ledge. Physical factors at the 43-km reef more closely resemble tropical reef systems (e.g., clear waters, with less temperature fluctuation due to proximity of the Gulf Stream), whereas the more turbid jetty and 8-km sites could be considered more “temperate.” Both offshore reefs support diverse assemblages of reef fishes at extremely high biomass and are long-term study sites of the National Undersea Research Center at the University of North Carolina at Wilmington (North Carolina, USA). Both temperate and tropical fishes occur on the offshore sites, but herbivorous parrotfishes and surgeonfishes that are common on tropical reefs are rare at our reef sites.

For several of our experiments, collections of *Ocu-*

*lina arbuscula* were made at an artificial reef (sunken ship)  $\approx 5$  km offshore from Atlantic Beach, North Carolina, at a depth of 10 m. *O. arbuscula* is the dominant benthic organism at this site, so many of the larger collections were made here to minimize impact on local populations at the other study sites.

#### General experimental methods

In most of the following experiments, a similar design was employed to test the effects of different factors (grazers, nutrients, seaweed removal, etc.), or combinations of factors, on coral growth. Because corals are clonal animals, colony growth can be used as a direct measure of fitness (Hughes et al. 1992). We collected small coral branches (4–5 cm tall) by breaking them off with a dive knife and kept them temporarily in running seawater tanks at the University of North Carolina Institute of Marine Sciences in Morehead City, North Carolina. No data are available on juvenile growth rates or size–age relationships in *Oculina arbuscula*, but 1-yr-old recruits that we followed in the field were  $< 1$  cm tall. We therefore surmise that our experimental transplants may be analogous to 5-yr-old, or older, juveniles. Corals were blotted with paper towels to remove excess water, weighed, and individually marked, either by tying  $3 \times 5$  mm numbered tags to the corals with nylon thread (tags from Floy Tag Company, Seattle, Washington, USA) or by numbering the polyvinyl chloride (PVC) plates onto which the corals were glued (see individual experiments, below). We then transplanted these pre-weighed branches into experimental conditions in the field.

At the end of an experiment we collected and re-weighed the corals. In all cases, recovery of corals at the end of an experiment was  $< 100\%$ , due to loss of the coral, loss of the numbered tag, breakage, or mortality. Thus, most experiments ended with an unbalanced design. In all of the caging experiments we placed multiple colonies in each cage to allow for loss, and to provide multiple subsamples from the relatively small number of independent replicates that was logistically feasible (usually about 10 replicates). In these cases, we do not argue that the growths of colonies within a single cage are independent, and so have used the mean of growths from multiple colonies in a single cage as one experimental observation. In these cases, the sample sizes we report are numbers of independent cage means, not numbers of corals.

In all the caging treatments, we used a mesh (1.5–2 cm openings) of very-fine-gauge plastic material that intercepted only  $7.9 \pm 0.07\%$  (mean  $\pm 1$  SE,  $n = 5$  cages) of the incoming photosynthetically active light and thus minimized both shading and effects on water flow. The relatively large openings in the mesh also excluded large herbivorous fishes and urchins while allowing access by smaller predatory fishes such as wrasses and blennies. Access by these smaller fishes should have minimized potential artifacts resulting

from cages providing predation refuges for mesograzers such as amphipods (see Lewis 1986).

We checked for gross violations of homogeneity of variances among groups by Cochran's or  $F_{\max}$  tests (Winer et al. 1991) and sought beneficial transformations when appropriate. To distinguish the main effects and interactions of experimental factors, analyses of variance were conducted on means of coral growths from each cage. In cases where the design was unbalanced, the significance levels reported here are from the Type III sum-of-squares estimates from the GLM procedure of SAS (SAS Institute 1985).

#### Natural distribution

To determine whether natural distributions of *Oculina arbuscula* and co-occurring seaweeds suggested that competition might be occurring, we conducted observational sampling at two different spatial scales. We measured coral density and seaweed percentage cover at eight offshore reef sites and two depths on jetties at both Radio Island and Cape Lookout (see Table 1). On three of these reefs (numbers 8, 10, and 11 from Table 1), as well as four additional reefs nearby, we also determined coral densities along the edge of the reef dropoff for seaweed-dominated horizontal substrates vs. immediately adjacent vertical substrates where seaweeds were uncommon.

*Within site.*—To determine the natural distribution of *O. arbuscula* and its potential negative association with seaweeds within a habitat, we sampled transects along two depth strata at Radio Island Jetty in September 1992. The shallow (1 m deep) transect was dominated by seaweeds. Due to the turbid conditions at this site, a transect along the bottom of the jetty, though only 6 m deep, was below the euphotic zone, and so seaweeds were absent.

A  $50 \times 50$  cm quadrat fitted with a monofilament grid yielding 100 random points was used to sample the abundance and size of coral colonies and estimate the percentage cover of other potentially competing benthic organisms. Colony size was estimated by placing a transparent grid of 1-cm<sup>2</sup> squares over the colony and estimating projected surface area. Quadrats were sampled at 26 randomly determined intervals along a 60-m transect at each depth.

Data were analyzed by *t* test to determine differences between depths in coral abundance (number of colonies/0.25 m<sup>2</sup>), seaweed abundance (percentage cover), and colony size (in square centimetres). We also calculated correlations of coral abundance in quadrats from the 1 m depth with percentage cover of seaweeds and in quadrats from the 6 m depth with percentage cover of other sessile invertebrates that might compete with corals.

*Among sites.*—To assess the distribution of *O. arbuscula* and its association with seaweeds on a regional scale, we sampled nine additional sites of diverse habitat types for coral abundance and seaweed cover. These

TABLE 1. Characteristics of North Carolina (USA) sites sampled for coral and seaweed abundance.

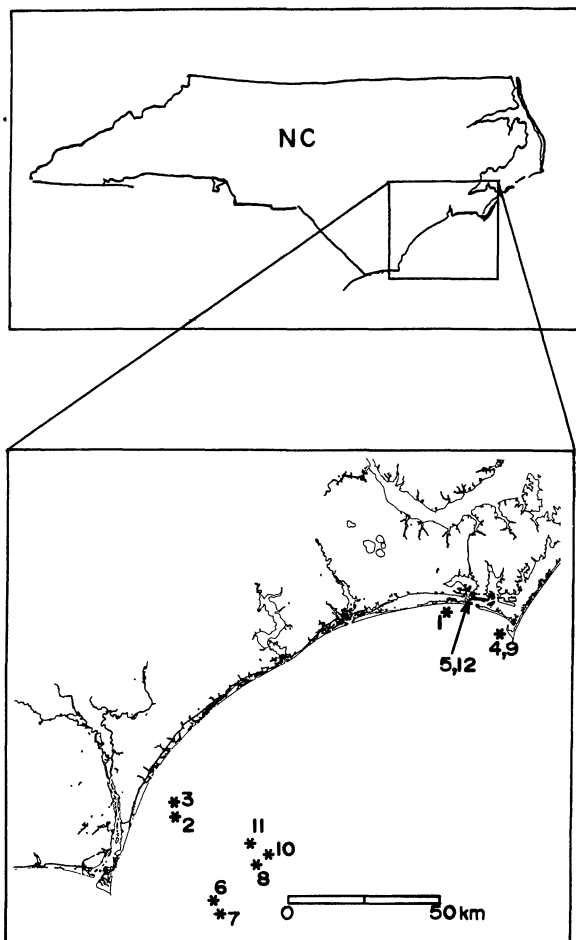
Site no.†	n‡	Name	Location§	Depth (m)	Distance (km)
1	11	Liberty Ship	34°41'10" N, 76°43'30" W	10	5
2	11	S-35	27259.0/39064.1	20	11
3	15	8-km reef	27262.0/39067.0	18	8
4	14	Cape Lookout Jetty (8 m)	27087.5/39680.0	8	0
5	26	Radio Island Jetty (6 m)	34°42'15" N, 76°41'00" W	6	0
6	6	S-38	27217.9/39052.6	25	29
7	10	S-40	27204.3/39051.3	25	34
8	10	Rass-23	27188.4/39153.4	23	43
9	14	Cape Lookout Jetty (2 m)	27087.5/39680.0	2	0
10	10	38-km reef	27186.0/39157.2	23	43
11	5	S-34	27190.6/39154.1	25	41
12	26	Radio Island Jetty (1 m)	34°42'15" N, 76°41'00" W	1	0

† Site numbers are as in Figs. 1 and 4.

‡ No. of quadrats sampled.

§ Latitude and longitude coordinates or LORAN coordinates.

|| Approximate distance from shore.

FIG. 1. Map of North Carolina (NC) sites surveyed for abundance of *Oculina arbuscula* and percentage cover of seaweeds. Names and locations of sites are given in Table 1.

sites consisted of deep (8 m) and shallow (2 m) habitats at one additional inshore jetty (Cape Lookout, North Carolina, October 1992), the 10 m deep artificial reef collection site (September 1993), and seven natural rock outcrop reefs (18–25 m deep) offshore of North Carolina, including the 8-km and 43-km sites (October 1993). The location and some characteristics of each site are given in Table 1; approximate locations are shown in Fig. 1. We sampled from a haphazardly placed transect along the rock ledge, the jetty, or the top of the artificial reef. Due to bottom time restrictions associated with diving at some of these depths, variable numbers of 0.25-m<sup>2</sup> quadrats were sampled at each site ( $n = 5$ –26 quadrats; see Table 1); quadrats were assessed at 3-m intervals along each transect. We conducted linear regressions with mean coral abundance at each site as the dependent variable to assess the ability of seaweed cover, depth, and distance from shore to explain variance in the abundance of *O. arbuscula*.

Lastly, because we found no coral colonies in the quadrats we sampled at the 43-km reef, we conducted additional sampling at the 43-km reef and six other similar reef ledges (25–28 m depth at the top, and having high seaweed cover) to determine whether corals were rare or absent (possibly indicating larval limitation) from these offshore sites. At each of these sites, we sampled two 50 × 1 m band transects, one along the horizontal top surface of the ledge where seaweeds were abundant, and one along the vertical side face of the ledge where seaweeds were much less abundant. Each of these 50-m<sup>2</sup> areas were carefully examined for any *O. arbuscula* colonies. A paired sample *t* test ( $n = 7$  sites) was used to determine whether corals were more common on the tops or sides of these reefs.

#### Direct effects of seaweeds on coral growth

The sampling described above could show negative associations of corals and seaweeds, and thus suggest

that competition might be occurring. However, we conducted three direct experimental tests to determine whether seaweeds exerted a competitive influence on *Oculina*. Two tests were conducted at the Radio Island Jetty site (summer and winter) and one at the 43-km reef site. We did not conduct this test at our turbid nearshore site (8-km reef) because seaweed cover there was very low (estimated at <10%).

**Radio Island, summer.**—In an initial summer experiment at Radio Island, we removed the seaweed canopy in patches along the top of the jetty at a depth of 1 m (MLW). We glued (with two-part PolyPox [Pettit Paint Company, Rockaway, New Jersey, USA]) preweighed coral branches collected from separate colonies at Radio Island onto numbered PVC plates ( $\approx 3 \times 3$  cm) and transplanted these into the cleared patches or adjacent patches with the natural canopy left intact (i.e., controls) by tying the plates to natural jetty rocks. Experimental patches were weeded at least weekly throughout the 11-wk experiment (August through October 1991), after which we re-weighed the corals. Data were evaluated by a Wilcoxon two-sample test ( $n = 10$ , 11 cleared and control patches, respectively).

**Radio Island, winter.**—Because the algal community shows marked seasonal variation at Radio Island, with common temperate genera (e.g., *Punctaria*, *Petalonia*, *Ectocarpus*, *Polysiphonia*) becoming abundant in winter, we repeated this experiment at the same depth during winter. In this experiment we used 14  $50 \times 60$  cm concrete slabs hosting a 9-mo-old seaweed canopy and removed this canopy with metal scrapers from one half of each slab. In February 1994, 14 tagged corals collected from the artificial reef site were cable-tied to metal pegs set in the slabs within the algal canopy and 14 to pegs in the halves of the slabs that were weeded weekly. The corals were collected after 8 wk for reweighing and analysis of weeding effects by a Wilcoxon two-sample test ( $n = 11$ , 12 corals recovered from scraped and from weeded slabs, respectively).

**43-km site.**—*Oculina arbuscula* occurs at extremely low density at the 43-km site (seven colonies in  $100\text{m}^2$ , with only 1 of these colonies being on the seaweed-dominated horizontal substrates, see *Results*), and seaweed abundance is extremely high. To determine if competition from the dense algal canopy could account for this relative rarity of corals, we conducted an experiment there from June through September of 1993. In addition to seaweed removal, this experiment involved placing corals on the sand veneer substrate and at an elevation of 15–20 cm above the substrate to test an alternative hypothesis that sand scour may restrict coral abundance at this site.

Twenty pairs of 20 cm tall galvanized nails were driven into the rock substrate, which was naturally covered with a 0–5 cm sand veneer. Paired nails were  $\approx 1$  m from each other and  $>2$  m from adjacent pairs. We removed the seaweed canopy from a 50 cm radius surrounding one of each pair and left the canopy intact

around the other. Two previously weighed and individually numbered coral pieces collected from the artificial reef site were attached with cable ties directly onto each nail. One was attached at the base of the nail, where it could experience sand scour, and one at the top of the nail, 12–15 cm above the substrate, where sand scour would not occur. Thus, the two experimental factors were weeding (presence or absence of seaweed canopy) and elevation (level with the sand or elevated), with 20 replicates of each of the four treatment groups. We weeded the cleared patches every 2–3 wk and collected and re-weighed the corals 14 wk later. We used a two-factor, model I ANOVA to test for significant effects of seaweed removal, elevation (sand scour), or an interaction of the two on coral growth (percentage change in wet mass).

#### *Effect of caging on coral growth and seaweed community structure*

Exclusion of grazers on tropical coral reefs results in profound alterations in benthic community structure, including replacement of corals and other benthic invertebrates with seaweeds (Hay and Taylor 1985, Lewis 1986, Hughes et al. 1987, Lessios 1988, Hughes 1989). We conducted caged grazer-exclusion experiments at all three of our experimental sites to determine whether coral–seaweed competition in these temperate habitats was moderated by grazing. We examined coral growth responses and seaweed abundance and species composition in grazer-exclusion cages and in open-sided cage controls.

**Offshore sites.**—As part of a larger, 3-yr project examining the effect of fish grazing on the development of benthic communities on temperate reefs (M. E. Hay, *unpublished manuscript*), 10 pairs of  $50 \times 60$  cm artificial substrates (concrete slabs) at each offshore site (i.e., the 8-km and 43-km sites) were fitted with individual fish-exclusion cages and open-sided (roof with only two walls) cage controls made of 2 cm plastic mesh. In 1991 and 1992 the full cages fit over the top of a 70-cm-tall frame of steel reinforcing bar and the cage controls had two of the side walls removed. Care was taken to align the two walls of the open cages perpendicular to the direction of predominant flow and surge (i.e., parallel to the ledge) to provide the best possible control for flow obstruction by the cages. By 1993 the steel frames were rusting through and breaking. Thus, in 1993, cages were basket-like structures, into which the slabs were placed. A full roof created a full cage, while a partial roof (2 mesh strips, each 15 cm wide) allowed access by fish through three openings in the cage top that were  $\approx 10 \times 50$  cm. Urchins were very rare at the 43-km site ( $\ll 1$  urchin/ $100\text{m}^2$ ). At the 8-km site they were common, but were consistently removed from reef areas near the slabs as part of a separate project (M. E. Hay, work in progress). Fishes were thus the main consumers affected by cages at these sites.

In all years, each cage held two flat (750-cm<sup>2</sup>) cinder blocks with small holes drilled through them so that they fit over metal pegs embedded into the base of the concrete substrate. Because these blocks could be removed and brought to the surface, it was on these blocks that seaweed abundance and other sessile community parameters were assessed (see *Coral Recruitment*, below). In 1991 and 1992 two new blocks were placed on each of the slabs at the start of the season. In 1993 one new block was placed on the substrate at the beginning of the experimental season and one remained from the 1992 growing season; this block thus supported a seaweed canopy that was already 1 yr old.

Coral growth was measured in these cages during the summers of 1992 and 1993. During each summer we transplanted four pre-weighed coral pieces into each cage. In 1992 transplanted corals were collected from the 8-km site and glued onto numbered PVC plates that were attached with cable ties onto a metal rod embedded in the concrete base near the side of the cage. Corals were transplanted in June and re-collected in October (18 wk later). In 1993 the corals were collected at the artificial reef site, fitted with numbered tags, and attached directly with cable ties (i.e., no PVC plate) to the metal rod in the concrete base of the cage. We collected and re-weighed corals after 21 wk (May through October). Mean growths of coral subsamples ( $\leq 4$ ) from the same cage were used as the observations in a three-factor ANOVA ( $n = 8$ –10 cage and half-cage pairs) on sites, years, and cage treatments followed by post-hoc pairwise comparisons (following the recommendations of Day and Quinn 1989) to determine the effect of caging within Site-Year combinations. In this three-factor analysis, we chose to treat year as a fixed, as opposed to a random, factor because we were interested in relating variation in coral growth in these particular years to variation in abundance of benthic competitors in these specific years (Sokal and Rohlf 1981; see *Results*, below). We determined biomass (as grams dry mass) of fleshy algae and other, potentially competing, sessile invertebrates at the end of each season by harvesting the sessile community from one of the cinder blocks in each cage, sorting organisms to species, and determining their dry mass. Dry mass of fleshy seaweeds was also analyzed by three-factor ANOVA (Cage  $\times$  Site  $\times$  Year).

**Radio Island.**—To test the effect of large grazers on *Oculina arbuscula* inshore, and whether this effect might be direct or indirect via change in the algal community, we independently manipulated algal abundance and grazing in a factorial experiment at Radio Island in the summer of 1992. Frames made of 20-cm-tall steel reinforcing bar (for cage support) were attached to 80 flat cinder blocks (38  $\times$  18  $\times$  4 cm) and placed in groups of four along the top of the jetty (1 m depth) in May 1992. Placement of the blocks was haphazard due to the unevenness of the jetty rocks, but each individual cinder block ranged from 0 to 20 cm

TABLE 2. Total percentage cover of seaweeds on blocks after the 1992 Radio Island experiment.

	Full cage		Open cage	
	$\bar{X}$	1 SE	$\bar{X}$	1 SE
Weeded	28.8	5.0	5.3	1.6
Unweeded	66.4	6.5	23.8	4.7
$P^\dagger$	<0.0001		0.0011	

$^\dagger$   $P$  values are from Mann-Whitney  $U$  tests of weeded vs. unweeded blocks in full and in open cages;  $n = 19$  groups of paired cages.

distant from the other three in its group and the groups of four blocks were at least 1 m apart. In June, after a month's delay to allow initial algal settlement, we glued corals onto PVC plates and attached (with cable-ties) four plates onto each experimental substrate. Two of each group of four blocks were fully enclosed in lightweight plastic 2-cm mesh to exclude larger grazers (fish and urchins), while the other two had the narrow ends of the cage open to serve as cage controls. At weekly intervals we hand-weeded and used metal scrapers to remove as much algal biomass as possible from one full cage and one open cage of each set. This weeding procedure significantly reduced algal cover both in full ( $P < 0.0001$ , Mann-Whitney  $U$  test,  $n = 19$  pairs of cages) and in open cages ( $P = 0.0011$ , Mann-Whitney  $U$  test,  $n = 19$ ), as shown in Table 2. We also maintained and cleaned the cage material routinely throughout the experiment. All mesh material was replaced midway through the experiment to minimize fouling and ensure the integrity of the cage exclusion. We maintained 20 independent replicates of our four treatments for 18 wk (June through mid-October). In addition to assessing coral growth at the end of the experiment, we also used a grid of 100 points to estimate the percentage cover of red and brown seaweeds (greens were rare) in each cage by counting the fraction of the points contacting each type of seaweed. We used a two-way fixed-factor ANOVA to determine effects of weeding, caging, and any possible interaction on coral growth.

#### *Interactive effects of grazing and nutrient addition*

We examined the possible combined or interactive effects of nutrient enhancement and grazing on the growth of *Oculina arbuscula* in a single two-way factorial experiment conducted during summer 1993 at Radio Island Jetty. The experimental factors were a caging treatment to exclude large grazers (primarily the omnivorous spottail pinfish, *Diplodus holbrooki*, and the purple sea urchin, *Arbacia punctulata*) and a nutrient treatment that involved periodic incubation in elevated nutrient conditions.

In March 1993 we placed 30 concrete slabs adjacent to the jetty on a sand bottom at a depth of 1–2 m. Each slab was 50  $\times$  60 cm and had an attached 50-cm-tall

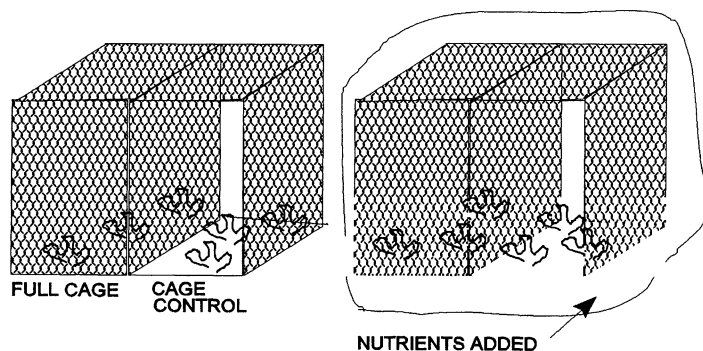


FIG. 2. Schematic design of one replicate for nutrient  $\times$  cage experiment at Radio Island Jetty, North Carolina, in 1993. Fourteen such replicates were maintained with three coral pieces in each cage unit (see *Methods: Interactive effects of grazing and nutrient addition*).

frame of steel reinforcing bars to support the cage structures. Natural colonization of the slabs, primarily by seaweeds, was allowed to proceed until mid-July at which time we installed plastic-mesh ( $1.5 \times 2$  cm openings) cages by sliding them over the metal reinforcing-bar frames and securing them around the bottom of the slab with bungee cords. The cage structures were constructed in such a way that each slab had a plastic-mesh wall down the center dividing a fully caged half (to exclude fish and urchins) from a half with a top, two sides, and two open sides that allowed access by consumers (cage control, see Fig. 2). We glued three pre-weighed and tagged coral pieces directly to each slab half using Z-Spar Splash Zone Compound (Koppers Company, Inc., Commerce, California, USA). Thus, one side of each slab constituted a caged treatment and the other side a cage-control treatment. Slabs were arranged in pairs, one that received elevated nutrient incubations and one that did not, as illustrated in Figure 2. Each pair of slabs, then, constituted one independent replicate in a split-plot design (one slab containing both levels of the cage treatment but only one level of the nutrient treatment), and 14 such replicate pairs were maintained.

We performed nutrient incubation treatments by placing a large plastic bag ( $0.28 \mu\text{m}$  [1.1 mil] thickness) over the slab and cage structure at slack high tide and sealing the bottom with the bungee cord. Approximately 170 g of garden fertilizer (Peters All-purpose, 20:20:20 N:P:K, Grace-Sierra Horticultural Products, Milpitas, California, USA) was mixed into 1 L of seawater and added to the nutrient addition treatments. At the end of slack tide the bags were removed, yielding a 1–2 h incubation. Tidal currents at this site are extremely strong and the high nutrient concentration in the incubation treatments was assumed to be diluted immediately after the bags were removed at the end of the incubation period (on an outgoing tide). Some local seaweeds can very rapidly take up enough nutrients for several days' worth of growth and so are able to increase their growth rates following these types of short-term nutrient pulses (Ramus and Venable 1987). Controls for the restricted water movement of the nutrient incubation consisted of placing the sealed bags over the control slabs for a similar period of time. Because

of time constraints associated with the short duration of slack tide, these bag controls were usually performed on the day following the nutrient additions. By reducing the number of bags that we installed on each occasion (i.e., by performing nutrient additions and controls on different days) we were able to maximize the duration of each treatment during the short slack-tide period. We performed nutrient incubations on days 15, 21, 28, 49, 51, 55, 59, 66, 70, and 78 of the 83-d period that the corals were in place (early August to mid-October). The hiatus between days 28 and 49 was due to the impending Hurricane Emily and complications resulting therefrom. The effectiveness of elevating nutrient concentration inside the bags probably varied inversely with the degree of wave turbulence, which on three or four occasions reached sufficient levels to shred the plastic bags.

To determine whether adding nutrients was increasing algal growth, we transplanted, on three different occasions, pre-weighed brown seaweeds onto each of the slabs the day before a nutrient incubation was conducted, collected these 1 wk later, and measured growth as increase in mass. On the first occasion *Dictyota* sp. was used; *Sargassum filipendula* was used on the other two occasions. These plants were intended to serve as "phytometers" to assay for elevated seaweed growth on the slabs that received nutrient addition.

At the end of the experiment we assessed coral growth and several characteristics of the seaweed community on the slabs. Percentage cover of the six most common genera of seaweeds (Browns: *Sargassum*, *Dictyota*, and *Padina*; reds: *Hypnea*, *Chondria*, and *Gracilaria*) was estimated using a grid of 100 random points. These seaweeds comprised virtually 100% of algal standing stock. Also, a subsample of the area of each half slab (the front  $8 \times 15$  cm corner of the slab) was harvested and sorted by genus. Wet mass of each genus was determined after being spun in a salad spinner (seven spins of the handle) to remove excess water. Six different split-plot, two-factor ANOVAs ( $n = 14$ ) were conducted on cover and on biomass of three composite variables, total red algae, total brown algae, and total algae of both types.

We also conducted a two-factor ANOVA ( $n = 14$ ) with split-plot design to test for significant effects of



nutrient addition, caging, and their interaction on coral growth. We could thus compare whether coral growth displayed patterns of variation amongst treatment groups consistent with those observed for the various algal parameters (i.e., high coral growth corresponding to low seaweed abundance and the converse).

#### *Coral recruitment*

We examined coral recruitment patterns at all three experimental sites to determine whether this process contributed to the observed distribution of *Oculina* on North Carolina reefs. At the offshore sites the effects of grazer exclusion on coral recruitment was observed during three different years. At the Radio Island Jetty site we examined the effects of depth and seaweed removal on the distribution of coral recruits.

*Offshore sites.*—We determined the number of *Oculina* recruits on the concrete substrates of the paired control and grazer-exclusion cages at both the 8-km and the 43-km sites in the autumns of 1991, 1992, and 1993. In 1991 recruitment was extremely high, so the number of recruits was subsampled. A polystyrene template with six randomly located  $5 \times 5$  cm openings was placed over each block, and the number of recruits in the openings summed (i.e., 150 cm<sup>2</sup> total for each replicate). In 1992 and 1993 recruitment was lower and all recruits on one of the two 750-cm<sup>2</sup> cinder blocks in each cage were counted. For comparisons, all data were converted to number of recruits/150 cm<sup>2</sup>. Three-factor ANOVA ( $n = 9$ –10 cage/half-cage pairs) was used to determine the significance of variation among cage treatments, sites, and years followed by post-hoc tests to determine cage effects within Site-Year combinations. Again, year was chosen to be a fixed instead of a random factor because our interest was in relating recruitment variation in these specific years to competitive conditions in these years.

Other benthic organisms in the treatment cages were also monitored (by harvesting one cinder block at the end of each season) and analyzed for correlative patterns. Dry mass of barnacles was used in a three-factor ANOVA (Cage  $\times$  Site  $\times$  Year). However, in 1993 several of the harvested samples spoiled, reducing sample sizes to  $n = 9$  and 7 (from 10 each) for full and half cages, respectively. Since percentage cover data were available for all 10 replicates in each treatment, we estimated barnacle dry mass according to a regression equation derived from actual barnacle mass and cover data measured in 1992 (mass =  $23.95 + 1.79\text{cover}$ ,  $R^2 = 0.827$ ,  $n = 20$  cage samples). These estimates from the 1992 data yielded means that were not different from the means of the actual mass data collected in 1993 (full cage estimate was  $123.1 \pm 13.3$  g [mean  $\pm 1$  SE] while actual was  $120.8 \pm 26.1$  g; half-cage estimate was  $112.8 \pm 8.1$  g while the actual was  $102.6 \pm 30.5$  g when means for the 16 pooled actual samples were compared with estimates for these samples cal-

culated using % cover,  $P = 0.782$ , Wilcoxon signed-ranks test,  $n = 16$  cage samples).

*Radio Island.*—At the Radio Island Jetty site we conducted a separate experiment to examine the effects of depth and seaweed canopy on coral recruitment. Ten flat cinder blocks ( $38 \times 18 \times 4$  cm) were placed at Radio Island Jetty in early August 1993 under each of three treatments: (1) 6 m deep, which is below the depth of upright seaweeds at this site, (2) 1 m deep with seaweed canopy left intact, and (3) 1 m deep with the canopy around the block removed. These treatments were designed as two planned comparisons to determine the effect of depth (treatment 1 vs. 3) and the effect of canopy (treatment 2 vs. 3) on coral recruitment. These treatments were imperfect in that blocks in the shallow “weeded” treatment still developed a covering of filamentous algae, and the blocks in the shallow “with canopy” were, themselves, relatively large uncolonized islands that had an algal canopy around them, but not on them. The number of recruits on each block was counted in November 1993. A  $t$  test between the shallow weeded treatment and the deep treatment was used to determine the importance of depth, while a separate Wilcoxon signed-ranks test (due to non-normality) compared the shallow weeded and the shallow with-canopy treatment to determine the effects of seaweeds on coral recruitment.

## RESULTS

### *Natural distribution*

*Within site.*—Coral abundance and seaweed cover were negatively correlated within a site. On Radio Island Jetty, density of *Oculina arbuscula* was a significant 70% higher on deeper (6 m) portions of the jetty where seaweeds were absent than on shallow (1 m) portions of the jetty where seaweeds were common ( $P = 0.05$ ,  $t$  test,  $n = 26$  quadrats, Fig. 3). Mean size of colonies also differed significantly between depths, with deep colonies having projected surface areas that were 114% larger than shallow colonies (mean  $\pm 1$  SE =  $16.66 \pm 3.14$  cm<sup>2</sup> for deep and  $7.78 \pm 1.14$  cm<sup>2</sup> for shallow colonies,  $P = 0.016$ ,  $t$  test,  $n = 16$  to 20 colonies). On the shallow portion of the jetty, algal cover (mean  $\pm 1$  SE) was  $72 \pm 3\%$ , and algal cover was negatively correlated with coral abundance across the 26 quadrats we measured ( $r = -0.48$ ,  $P = 0.01$ ). Along the deep transect there were no seaweeds, and mean cover of other sessile invertebrates that might compete with corals was less ( $29 \pm 4\%$ ) than the cover of seaweeds on the shallow jetty. Cover of these other invertebrates showed some negative relationship with coral abundance, but this relationship was not significant and not as strong as for seaweeds on the shallow jetty ( $r = -0.37$ ,  $P = 0.06$ ,  $n = 26$  quadrats).

*Among sites.*—When we sampled *Oculina arbuscula* abundance and seaweed cover at 12 sites that ranged from 1 to 25 m in depth and from 0 to 43 km offshore,

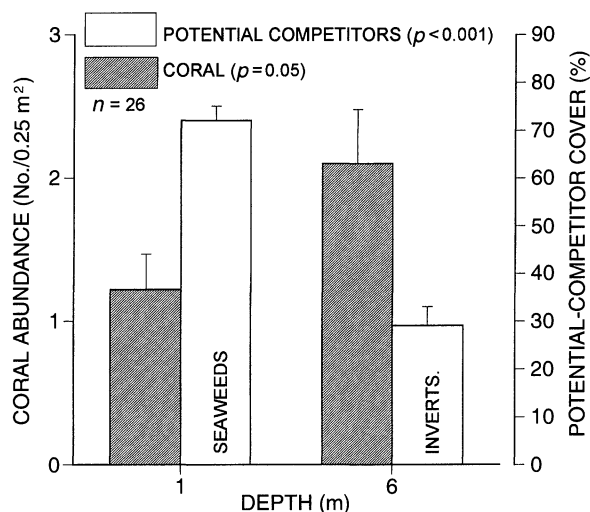


FIG. 3. Abundance (mean  $\pm$  1 SE) of corals and other sessile benthic organisms (seaweeds or other invertebrates) in 26 quadrats placed in both deep (6 m) and shallow (1 m) habitats at Radio Island Jetty (North Carolina) during September 1992.  $P$  values are from two-sample  $t$  tests comparing between depths.

we found a strong and significant negative relationship between corals and fleshy seaweeds ( $R^2 = 0.769$ ,  $P = 0.0002$ , linear least-squares regression, Fig. 4). This regression of coral abundance against seaweed cover provided a much better fit than was obtained from regressions of coral abundance on distance from shore ( $R^2 = 0.268$ ,  $P = 0.085$ ) or depth of site ( $R^2 = 0.0607$ ,  $P = 0.440$ ). Thus, of the parameters we measured, abundance of seaweeds was the clearest predictor of coral abundance on a regional scale.

Additional, more intensive sampling for the existence of *Oculina arbuscula* at seven offshore reef ledges demonstrated that, though rare, *O. arbuscula* was present at all but one of these sites, indicating that *Oculina* had recruited to almost all of these types of reefs. Significantly fewer colonies occurred along the tops of the ledges (mean  $\pm$  1 SE =  $0.286 \pm 0.184$  colonies/50 m<sup>2</sup>) where seaweeds were abundant than along the vertical faces of the ledges ( $3.71 \pm 1.149$  colonies/50 m<sup>2</sup>) where seaweed cover was low ( $P = 0.023$ , paired sample  $t$  test,  $n = 7$  ledges).

Overall, these descriptive data show that coral and seaweed abundance were negatively related on both local (in metres) and regional scales (10s–100s of kilometres). These patterns are consistent with the hypothesis that seaweeds competitively suppress corals on these high-latitude reefs.

#### Direct effects of seaweeds on coral growth

Field experiments demonstrated that seaweeds significantly reduced coral growth at both the shallow, inshore Radio Island Jetty site and the deep, offshore 43-km site.

**Radio Island, summer and winter.**—In summer at

Radio Island, corals placed 1 m deep in patches from which the seaweed canopy was removed ("weeded" treatment) grew a significant 560% more than corals placed within natural seaweed canopies at this same depth ( $P = 0.0001$ , Wilcoxon two-sample test, Fig. 5). Corals from the unweeded control treatment were pale, fouled by filamentous algae, and exhibited patches of dead tissue. These symptoms of stress did not occur for corals in the seaweed-removal plots.

In the winter at Radio Island, seaweed removal still enhanced coral growth by a significant 180% ( $P = 0.001$ , Wilcoxon two-sample test, Fig. 5) even though weekly weeding did not keep the weeded corals completely free from algal overgrowth. During winter, filamentous algae like *Ectocarpus* spp. drifted in the water column, caught on corals and other algae, and overgrew them. We commonly observed living corals in both the weeded and control groups being colonized by these filamentous algae in winter.

**43-km site.**—Data from a similar weeding experiment at the 43-km site, where we also manipulated coral height above the sandy bottom to evaluate effects of sand scour, showed gross violation of the assumption of homogeneity of variances between groups ( $F_{\max} = 18.7$ ,  $P \ll 0.01$ ). Due to the occurrence of negative growth observations in these data, we added a constant (10%, equal to the largest negative growth magnitude) to eliminate negative values before conducting an arcsine transformation. Transformation considerably improved heteroscedasticity ( $F_{\max} = 3.53$ ,  $0.01 < P < 0.05$ ), so we proceeded with analysis by two-factor

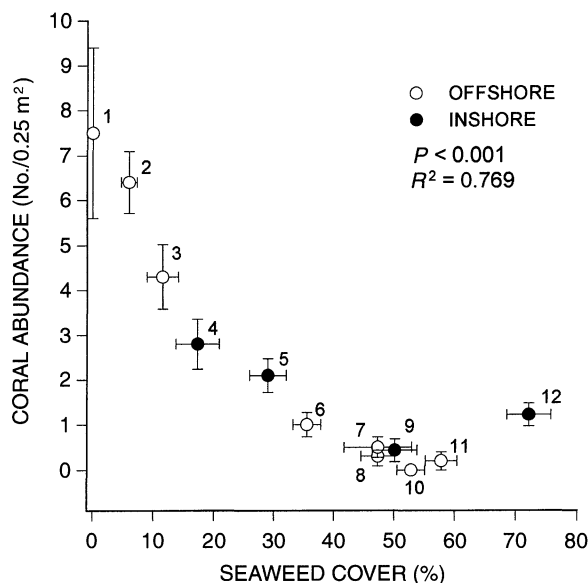


FIG. 4. Coral abundance as a function of seaweed cover at 12 North Carolina reef sites (see Table 1). Each point on the graph represents a mean ( $\pm$  1 SE) of 5 to 26 quadrats (see Table 1) sampled at each site (open) or each transect for the jetty sites (solid).  $P$  value is from linear least-squares regression.

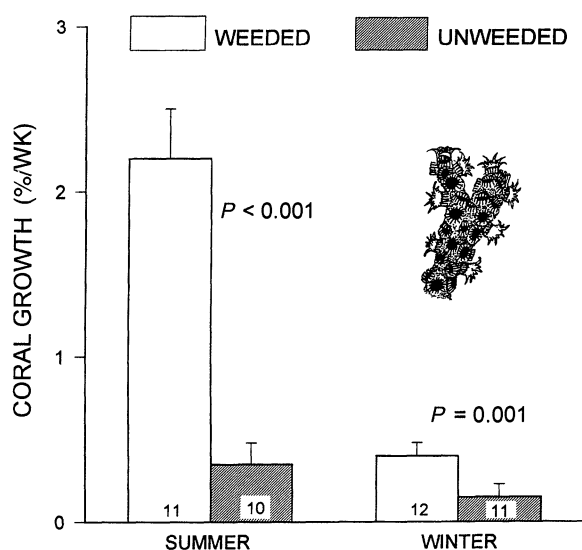


FIG. 5. Weekly growth of corals (percentage change in wet mass; mean  $\pm$  1 SE) in weeded and unweeded treatments (absence vs. presence of seaweed canopy) at Radio Island Jetty, North Carolina, during summer (1991) and winter (1994).  $P$  values from Wilcoxon two-sample tests; number of samples is given in each bar.

ANOVA on the transformed data. There was a significant interaction of weeding and height treatments in this analysis ( $P = 0.0197$ , Fig. 6, which plots original, not transformed, data), so the probability values associated with the main effects in the overall ANOVA are not interpretable. Over the duration of the experiment, corals in unweeded plots lost 2–4% of their wet mass, while those in weeded plots increased by 12–18% (Fig. 6). Weeding (main factor) significantly improved coral growth ( $P < 0.05$ ) in each of the height treatments according to Games-Howell post-hoc tests for simultaneous multiple comparisons (Day and Quinn 1989); the interaction is reflective of a larger magnitude of this enhancement of coral growth by weeding when corals were elevated than when they were even with the substrate. By contrast, the effect of height (main factor) differed in direction between weeded and unweeded treatments (Fig. 6) though neither of these paired comparisons (elevated vs. unelevated in the weeded plots and in the unweeded plots) were significant at the  $P = 0.05$  level. These patterns could be caused by greater negative effects of algal whiplash on elevated corals in unweeded plots and some negative effect of sand scour on non-elevated corals in weeded plots.

#### Effects of caging on coral growth and seaweed community structure

**Offshore sites.**—In the experiments excluding large grazers (primarily fishes) at both the 8-km and 43-km offshore sites, three-way ANOVA indicated a significant interaction of site and caging treatment ( $P = 0.032$ , Fig. 7A). This significant Site  $\times$  Cage interac-

tion resulted from the trend for caging to increase coral growth at the 8-km site while reducing growth at the 43-km site. Although the relatively powerful ANOVA procedure indicated significant effects in this experiment, the less powerful Tukey's post-hoc tests of the four paired-comparisons for cage effects (within Site-Year combinations) could not identify these effects at the  $P = 0.05$  level. Corals generally grew less at the 43-km site than at the 8-km site ( $P = 0.0238$  for Site, Fig. 7A); this pattern was strong in 1993, but less so in 1992. Also, corals grew significantly more in 1992 than in 1993 ( $P = 0.0001$  for Year).

In order to assess how seaweed mass might be affecting coral growth, upright seaweeds on one of two 750-cm<sup>2</sup> blocks in each cage in 1991 and 1992 were harvested (these consisted almost entirely of the common brown seaweeds like *Sargassum*, *Dictyota*, *Dictyopteris*, *Zonaria*, and *Lobophora*), dry mass determined, and this mass multiplied by two as an estimate of the amount of seaweed (on the two blocks) in each cage (Fig. 7B). In 1993, one of the two substrates in each cage remained from 1992, and contained a more mature algal canopy (see *Methods: Effect of caging . . . : Offshore sites*). In this case, data are given for the sum of seaweed mass on the old and new substrate for each cage (Fig. 7B). Three-factor ANOVA on square-root-transformed data showed that there was significantly more dry mass of seaweeds in open cages than in full cages ( $P = 0.003$ , Fig. 7B). This is the opposite of the pattern we would expect if grazing fishes were enhancing growth of corals by suppressing seaweed abundance, because grazing (open-sided cages) was asso-

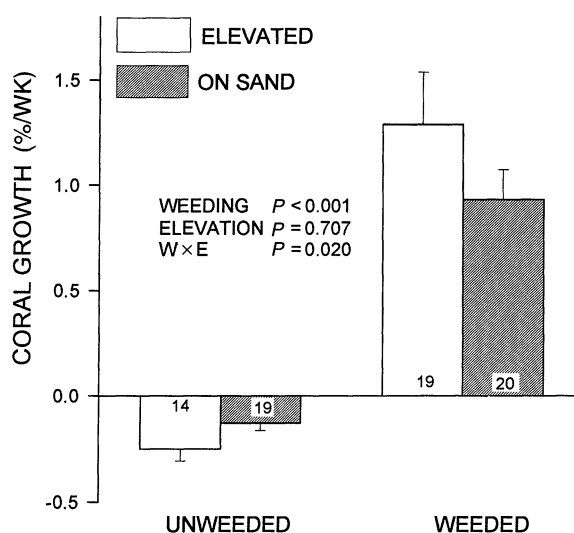


FIG. 6. Weekly growth (mean and 1 SE) of corals at the 43-km site under orthogonal conditions of seaweed canopy (weeded vs. unweeded) and elevation above the substrate (susceptibility to sand scour).  $P$  values from two-factor ANOVA (error df = 68, all others = 1); number of samples is given in each bar. Post-hoc comparisons indicate that weeding significantly improves coral growth in both elevated and "on sand" groups ( $P < 0.05$ ).

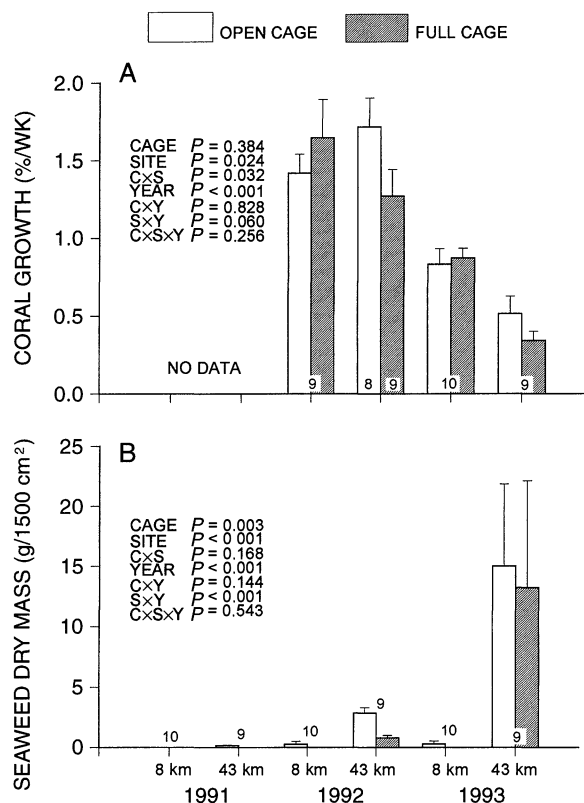


FIG. 7. Weekly growth of corals (change in wet mass) (A) and mass of fleshy seaweeds (B) in offshore grazer-exclusion cages at two sites in three different years. Data are means  $\pm$  1 SE; number of samples is given in each bar.  $P$  values are from three-factor ANOVAs on square-root-transformed data (for coral growth: error df = 65, all others: df = 1; for seaweed mass: error df = 99, df = 2 for Year, S  $\times$  Y, C  $\times$  Y, and C  $\times$  S  $\times$  Y, and df = 1 for all others).

ciated with greater coral growth at the 43-km site but greater, not lesser, total seaweed abundance. With the exception of the 43-km site in 1993, however, overall amounts of seaweed in both open and full cages were relatively small (Fig. 7B), low in height, and seemed unlikely to exert a competitive influence on corals.

The three-factor ANOVA on seaweed dry mass also showed significant effects of Site ( $P = 0.0001$ ), Year ( $P = 0.0001$ ), and the Site  $\times$  Year interaction ( $P = 0.0001$ , Fig. 7B). Seaweed biomass was always very low at the 8-km site (probably attributable to turbidity and low light) and significantly higher ( $P = 0.0001$  for Site), sometimes much higher, at the 43-km site. The significant Site  $\times$  Year interaction indicates simply that the magnitude of this difference was much greater in 1993. At the 43-km site, this extremely high seaweed mass in 1993 was associated with lower coral growth in 1993 than in 1992 ( $P = 0.0001$  for Year, Fig. 7A). This result may indicate that greater accumulation of algae in both types of cages in 1993 had a negative impact on corals. However, this is a correlative relationship, not an experimental effect, and therefore

needs to be interpreted cautiously. The significant differences in coral growth between sites ( $P = 0.024$ ) and between years ( $P = 0.0001$ , Fig. 7A), often were associated with large differences in algal biomass between sites and years. As in the more direct experiment reported above, these data suggest that when seaweeds are abundant (e.g., 1993 at the 43-km site), they can suppress coral growth. However, herbivorous fishes on these temperate reefs appeared to have no strong effect on the interactions between corals and seaweeds ( $P = 0.384$  for cage effect on coral growth, Fig. 7A). In fact, seaweed mass was significantly higher in open-sided cages available to fishes than in cages that excluded fishes ( $P = 0.003$  for cage effect, Fig. 7B).

**Radio Island.**—The factorial experiment at Radio Island examining the effects of both weeding and grazing also showed that experimental weeding significantly enhanced coral growth ( $P = 0.012$ ) while caging ( $P = 0.218$ ) and the interaction of caging and weeding ( $P = 0.450$ ) had no significant effects (Fig. 8). As in the experiments offshore, larger grazers did not directly impact coral growth at this site.

Caging did have a significant effect on seaweeds. Grazers caused a profound shift in the structure of the algal community from one dominated by relatively palatable red seaweeds (e.g., *Hypnea*, *Chondria*) to one dominated by unpalatable brown algae such as *Sargassum* and *Dictyota* (Fig. 9; see Hay et al. 1987, 1988 for data on palatability). By paired  $t$  tests, brown algae were significantly more abundant in open cage-controls than in full cages ( $P = 0.0005$ ) and the opposite was true of red algae ( $P = 0.001$ , Fig. 9). On the unweeded blocks the total percentage cover of seaweeds was significantly greater in full cages where large grazers were

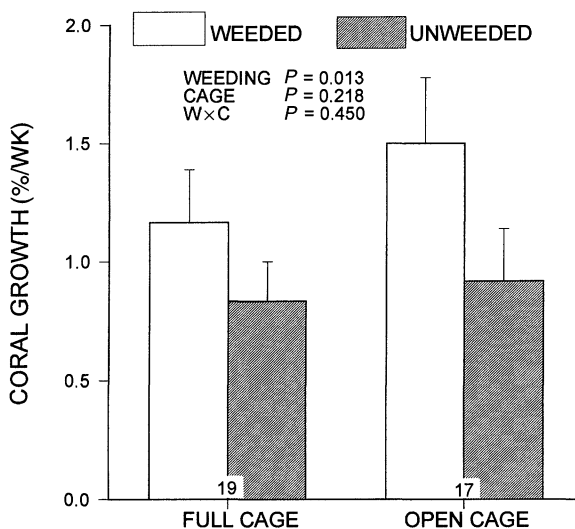


FIG. 8. Growth of corals (change in wet mass) under conditions of weeding and grazer exclusion at 1m depth, Radio Island Jetty, 1992. Data are means  $\pm$  1 SE; number of samples is given in each pair of bars.  $P$  values are from two-factor ANOVA (error df = 68, all others: df = 1).

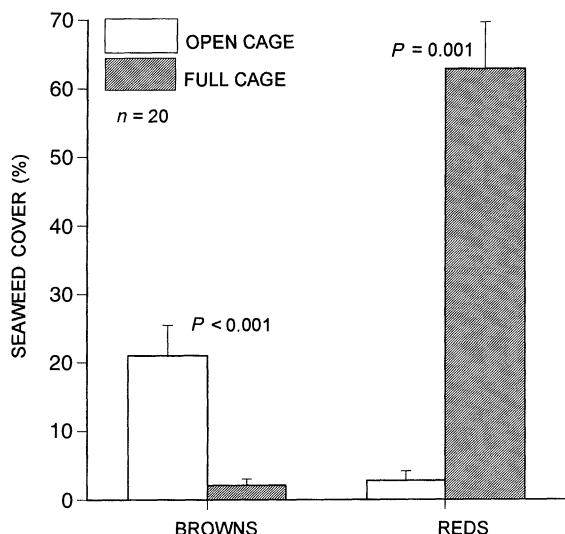


FIG. 9. Ending percentage cover (mean  $\pm$  1 SE) of red and brown seaweeds in unweeded full and open cages, Radio Island Jetty, 1992.  $P$  values from paired  $t$  tests;  $n = 20$  cages.

excluded than in open cage controls ( $66.4 \pm 6.5\%$  and  $23.8 \pm 4.8$  [mean  $\pm$  1 SE], respectively;  $P = 0.0001$ , paired  $t$  test).

#### Interactive effects of grazing and nutrient addition

In the two-factor experiment at Radio Island examining how nutrient enhancement might affect the above patterns, Cochran's test for heteroscedasticity indicated weak heterogeneity of variances among groups ( $C = 0.533$ ,  $0.05 > P > 0.01$ ). Arcsine transformation of the data, after addition of a constant to alleviate negative values, did not improve heteroscedasticity. ANOVA procedures are robust under moderate violations of the assumption of homogeneity of variances (Underwood 1981), so we proceeded with the analysis as planned on untransformed data, conducting a two-factor ANOVA for a split-plot design according to Winer et al. (1991) and SAS (SAS Institute 1985).

Fig. 10 shows the response of the six algal variables in this experiment (cover and biomass of red, brown, and red + brown algae). Caging did not significantly alter total algal biomass ( $P = 0.814$ ) or cover ( $P = 0.816$ ) but, as in the previous experiment, the red and brown components showed (significant) opposite trends, with red algal biomass dominating in full cages ( $P = 0.0001$  for cage effect) and brown algal biomass dominating in the open cages ( $P = 0.0001$  for cage effect, Fig. 10).

There was a significant interaction of nutrient addition and caging in determining red algal cover ( $P = 0.0469$ , Fig. 10), with nutrient addition resulting in significantly increased red algal cover in full cages. Thus, nutrient addition increases cover (but not mass) of red algae, but only if they are protected from con-

sumers. The same general patterns (i.e., enhancement by nutrient additions in full cages) were observed for wet mass of reds, but these patterns were not statistically significant. Nutrient addition had no significant effects (or interactions) on percentage cover or mass of brown algae growing on the cage substrates (Fig. 10), and we found no difference in growth of the brown seaweeds *Dictyota* or *Sargassum* when they were transplanted into the nutrient addition vs. control cages for periods of 7 d ( $P > 0.3$ , Table 3). The significant effects (Fig. 10) of Cage–Nutrient interactions seen for red algal cover (but not mass) or for total algal cover (but not mass) along with the significant main effect of nutrients for red algal cover (but not brown algal cover) suggest that nutrients affected red but not brown seaweeds and affected lateral spread of red algal clones more than they affected biomass accumulation.

Being in open cages increased coral growth in this experiment ( $P = 0.015$ , Fig. 11), especially when nutrients were added (Tukey's post-hoc comparison  $P < 0.05$ ). The nutrient addition alone did not cause significant effects on coral growth ( $P = 0.917$ , Fig. 11). However, there was a nonsignificant ( $P = 0.088$ , Fig. 11) interactive effect of caging and nutrient addition, corresponding to a pattern whereby the addition of nutrients was associated with higher coral growth in the open cages but lower coral growth in full cages (Fig. 11). This apparent pattern suggests that the impact of nutrient addition on coral growth depends on the presence of grazers. In combination with the algal cover patterns shown in Fig. 10, these patterns suggest that, at this shallow, well-lit site, nutrients increased red algal cover and thus caused decreased coral growth when herbivores were excluded. If herbivores were present, they consumed the palatable red seaweeds and prevented this seaweed–coral interaction.

#### Coral recruitment

The above experiments assessed how seaweeds and factors altering their abundance affected growth of coral branches that appeared similar to colonies that were 4 to  $>5$  yr old. Seaweeds and consumers also appeared to affect corals by impacting their recruitment at both offshore and inshore sites.

**Offshore sites.**—Coral recruitment in the offshore cages varied significantly by Cage treatment, by Site, and by Year ( $P = 0.0001$  for all main effects and interactions, Fig. 12A) as indicated by three-way ANOVA on square-root-transformed data. In 1991, recruitment in open-sided cages at the 8-km site was about 9 times greater than recruitment in full cages that excluded larger grazers ( $P < 0.05$ , Games-Howell post-hoc comparison). We observed no recruitment at the 43-km site in 1991, and very little in subsequent years (1992: mean of 0.4 recruits/750 cm<sup>2</sup> for open cages and 0 for full cages; 1993: no recruitment in either cage type). In 1992, overall levels of recruitment were much lower at the 8-km site (about one fifth); so, although

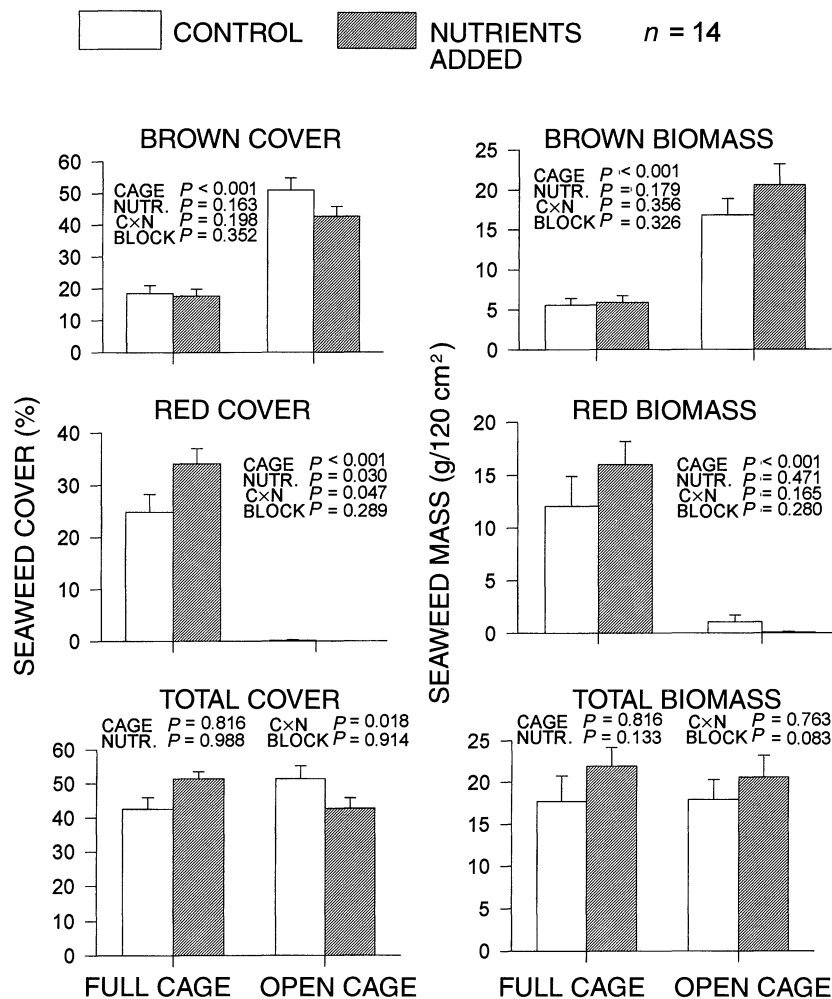


FIG. 10. Ending percentage cover and wet biomass of red, brown, and total (red+brown) algae under conditions of grazer exclusion and nutrient addition vs. control conditions at Radio Island Jetty, 1993. Data are means  $\pm$  1 SE;  $P$  values are from two-factor split-plot ANOVAs ( $df = 20$  for error, 13 for block, and 1 for all others);  $n = 14$  cages).

recruitment again appeared to be greater in open cages at this site, the difference was not statistically significant at the  $P = 0.05$  level (Games-Howell post-hoc comparison). In 1993 we again observed very low levels of recruitment at the 8-km site, and no significant cage effect (Fig. 12A). In summary, corals always recruited at the turbid, inshore site where adult colonies were common and seaweeds were rare. In years with

higher recruitment, open-cage treatments where grazers had access facilitated recruitment. In years with low recruitment, caging had no significant effect. Coral recruitment was always very low to non-existent at the better-lit 43-km site where seaweeds were plentiful and adult corals rare.

As in the offshore coral-growth experiments, it is difficult to attribute the significant cage effects, all at

TABLE 3. Results from three (1993) trials of examining growth of brown algal pieces in the nutrient addition and control treatments.

Trial	Alga	Dates	Growth†		$P$ ‡	$n$ §
			Nutrient addition	Control		
1	<i>Dictyota</i>	23–27 Aug.	60.7 $\pm$ 12.9	68.1 $\pm$ 6.8	>0.6	7
2	<i>Sargassum</i>	14–21 Sept.	75.9 $\pm$ 16.1	71.8 $\pm$ 15.5	>0.6	6, 8
3	<i>Sargassum</i>	1–8 Oct.	51.2 $\pm$ 3.6	54.5 $\pm$ 4.9	>0.8	13

† Percentage change in wet mass (mean  $\pm$  1 SE).

‡  $P$  values are from  $t$  tests (one-tailed if treatment > control; otherwise, two-tailed).

§ Number of plants.

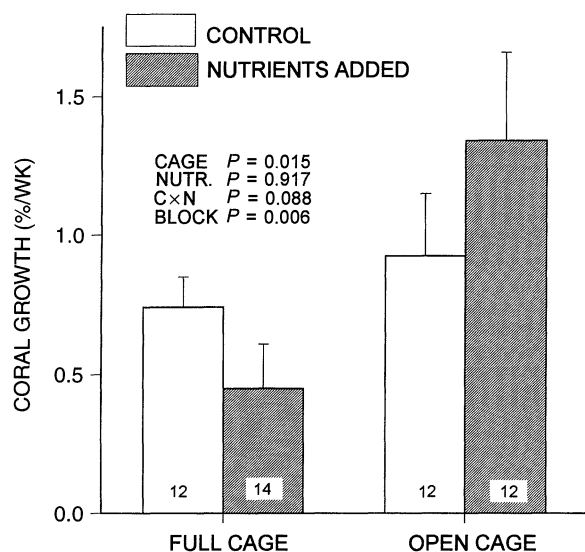


FIG. 11. Growth of corals (change in wet mass) under conditions of grazer exclusion and nutrient addition vs. control conditions at Radio Island Jetty, 1993. Data are means  $\pm$  1 SE;  $P$  values are from two-factor split-plot ANOVA (error  $df = 20$ , block  $df = 13$ , all others:  $df = 1$ ); number of cages is given in each bar.

the turbid 8-km site, to differences in seaweed abundance between cage treatments since seaweed abundance and cover were extremely low at this site regardless of cage treatment. We observed no significant difference in seaweed abundance, as measured by dry mass, between the full- and open-cage treatments at the 8-km site in either 1991 or 1992, and these abundances were always very small (Fig. 7B). In contrast, barnacles were abundant at the 8-km site and covered a majority of our experimental surfaces. Three-factor ANOVA on barnacle abundance (square-root transformed) showed all main effects and interactions to have a significant effect (Fig. 12B). Barnacle abundance was significantly higher in the full-cage than in the open-cage treatments at the 8-km site in 1991 and 1992 ( $P < 0.05$  for each), but no difference occurred in 1993 (Fig. 12B). There was a significant negative correlation between abundance of barnacles (dry mass) and number of recruiting corals in those years when barnacles varied by cage treatment ( $r = -0.432$ ,  $P = 0.006$ ,  $n = 36$  cages, when 1991 and 1992 are pooled). In the field, we observed fish (sheepshead, *Archosargus probatocephalus*) scraping barnacles from open-sided cages, and assume that they may have been responsible for generating these differences. In our open-sided cages it was common to see areas where only barnacle bases remained, their upper portions having been scraped away, apparently by these fish.

Patterns of seaweed abundance between the two offshore sites conform to predictions based on the hypothesis of seaweeds limiting coral recruitment. In all three years examined, seaweed standing stock was significantly higher at the 43-km site (Fig. 7B), where

coral recruitment was absent or negligible (Fig. 12A). In the turbid location where seaweeds were rare (i.e., 8-km site), corals recruited more heavily; however, at this site barnacles appeared to negatively affect coral recruitment.

**Radio Island.**—At Radio Island where seaweeds are abundant on the shallow jetty, we observed almost no recruitment in the shallow (1 m deep) treatment when the seaweed canopy was left intact. Only 1 replicate out of 10 (and it was adjacent to an adult colony) had recruits, resulting in an average recruitment of  $<1$  recruit per replicate (Fig. 13). Recruitment of corals on the shallow jetty increased by about a factor of 12 when the seaweed canopy was removed ( $P = 0.031$ , Wilcoxon signed-ranks test,  $n = 10$ ), reaching levels similar ( $P = 0.434$ , two-sample  $t$  test, Fig. 13) to those measured on the deep (6-m) portions of the jetty where seaweeds are absent and corals more abundant (Fig.

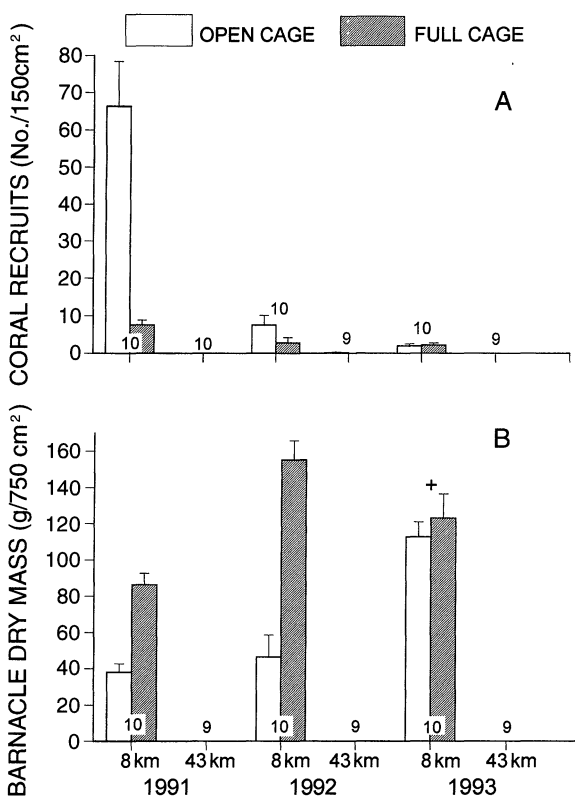


FIG. 12. Recruitment of corals (A) and dry mass of barnacles (B) in offshore grazer-exclusion cages at the 8-km and 43-km sites in 1991, 1992, and 1993. Data are means  $\pm$  1 SE. The number of cages is given in or above each pair of bars. Both of these three-factor ANOVAs (Site  $\times$  Cage  $\times$  Year) indicated great significance ( $P = 0.0001$ ) of all seven main effects and interactions ( $df = 103$ – $104$  for error;  $df = 2$  for Year,  $Y \times S$ ,  $Y \times C$ , and  $Y \times S \times C$ ; and  $df = 1$  for Site, Cage, and  $S \times C$ ). Post-hoc comparisons indicated that caging significantly inhibited recruitment at the 8-km site in 1991 ( $P < 0.05$ ). The "+" indicates that data shown for 1993 barnacle mass are estimated from percentage cover of barnacles (see *Methods: Coral recruitment*).

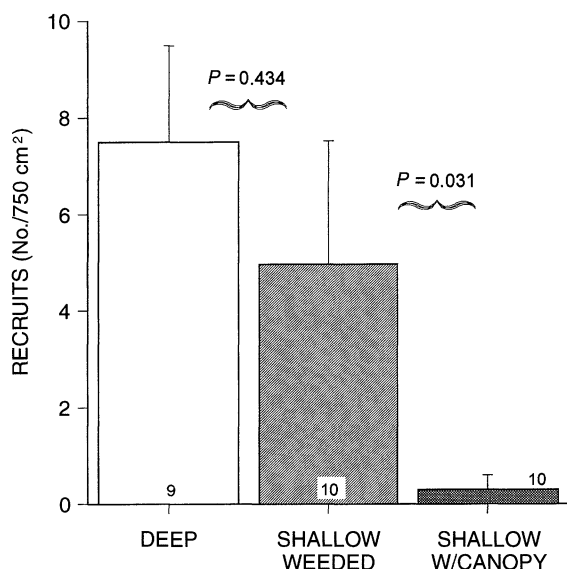


FIG. 13. Recruitment of corals (mean  $\pm$  1 SE) at Radio Island in 1993 in deep (6 m), shallow (1 m) weeded, and shallow with algal canopy (unweeded) treatments. *P* value for the planned comparison testing the effect of seaweeds is from a Wilcoxon paired signed-ranks test (shallow with vs. shallow without canopy) and that for effect of depth (deep vs. shallow without canopy) is from a two-sample *t* test. The number of substrates is given in or above each bar.

3). The highest average levels of recruitment and the highest proportion of replicates with recruits (78%, 60%, and 10% for the deep, shallow without, and shallow with canopy, respectively) were observed in the deep treatment.

#### DISCUSSION

Hundreds of studies have focused on patterns and processes affecting tropical reefs and the populations of corals that produce them (as examples, see the 263 papers in Choat et al. [1988], and the review by Jackson [1991]). Fewer have focused on coral reefs near the extremes of their latitudinal distribution (reviewed by Crossland 1988), and almost no information is available on temperate corals, how they persist in regions dominated by seaweeds, and what factors prevent their accumulation and, thus, production of coral reefs. Coyer et al. (1993) studied how the temperate coral *Balanophyllia elegans* was affected by seaweeds in California kelp beds. They observed that adult corals were often overgrown and killed by kelp holdfasts, filamentous algae, or coralline algae, and that overgrowth by filaments and corallines was facilitated when fronds of larger seaweeds chronically brushed against the corals. If sea urchins were abundant, their feeding removed macrophytes and protected corals from overgrowth. Our findings for *Oculina arbuscula* in the temperate Atlantic suggest that this coral also is limited by competition with seaweeds. Though *O. arbuscula* is not a reef-forming coral, this study identifies several

community-level factors that restrict its recruitment, growth, and distribution, and thus may help explain why this coral does not accrete at rates allowing reef formation.

#### Effects of seaweed competition

*Oculina* abundance and seaweed cover were negatively associated on both local and regional scales (Figs. 3 and 4). When comparing multiple reef habitats, corals were most abundant on turbid reefs with low abundance of seaweeds (Table 1, Fig. 4: sites 1–3, 3–10 km from shore). *Oculina* was extremely rare on shallow jetties, or on deep reefs in clear oceanic water, where algal abundance was high (Table 1, Fig. 4: sites 7–12). Thus, seaweeds dominated in well-lit habitats (shallow, or deep but with clear water), while *Oculina* were significantly more abundant in deeper, or more turbid, habitats (Figs. 3 and 4). This pattern was observed despite results from previous experiments showing that *Oculina* grew significantly better under high light in shallow waters, where *Oculina* rarely occurs, than under low light in deeper waters, where *Oculina* is more abundant (Miller 1995). Additionally, several studies have identified sedimentation and turbidity as detrimental to tropical corals (see Rogers 1990), yet *Oculina* was most abundant in sites that we subjectively classified as having high turbidity (e.g., the 8-km site and the artificial-reef site). This suggests that the negative effects, if any, of turbidity for this coral may be modest compared with the detrimental effects of competition with seaweeds in less turbid sites.

Our manipulative experiments demonstrated that corals could grow well in sites where they were absent or rare (e.g., offshore reefs or shallow areas of the jetty) if competition from seaweeds was reduced. Field experiments in a wide variety of habitats (inshore, offshore, deep, shallow, turbid, clear) and seasons (winter and summer) demonstrated that a seaweed canopy significantly and consistently inhibited coral growth (Figs. 5, 6, and 8) and recruitment (Fig. 13). In habitats where seaweeds were rare, barnacles also appeared to inhibit coral recruitment (Fig. 12), but it is doubtful that barnacles could affect growth (as opposed to recruitment) of the much larger corals once the corals were established.

We did not directly test the mechanisms by which seaweeds suppressed coral growth, but shading and abrasion could both be important. Previous studies on nutrition in *O. arbuscula* demonstrated that low light caused reduced growth and was associated with lower concentrations of chlorophyll *a* (Miller 1995). Thus, it is likely that the paleness of corals we observed under algal canopies indicated a detrimental effect of shading (i.e., exploitative competition for light). Whiplash by seaweeds also could be detrimental to *Oculina*. When *Oculina* are touched, polyps withdraw and are unable to feed; this response could compound the metabolic deficits caused by seaweed shading. Abrasion of a dif-



ferent temperate coral by seaweeds and plastic seaweed mimics has been shown to reduce coral activity levels and facilitate overgrowth of the coral by filamentous and coralline algae (Coyer et al. 1993). We observed similar colonization of live *Oculina* by filamentous algae in the with-canopy treatments of many of our experiments. Also, the tendency for elevated corals in the offshore experiment to fare worse than corals at ground level when algal canopy was present, but better when the canopy was removed (Fig. 6), suggests that whiplash by seaweeds may have been differentially affecting the elevated colonies. Thus, it seems that both exploitative and interference competition may occur between seaweeds and *Oculina arbuscula*.

At the 43-km reef site where both seaweeds and sand scour could have been excluding corals, competition from seaweeds had a greater effect than sand scour (Fig. 6). Transplanted coral fragments grew well in weeded plots whether they were subject to sand scour or elevated above the sand, while coral fragments in unweeded plots exhibited a net loss of mass both with and without the potential for sand scour. The significant interaction ( $P = 0.02$ ) of the weeding and elevation treatments in this experiment occurred because elevation increased coral growth in weeded plots but decreased coral growth (possibly due to whiplash) in unweeded plots.

On the reefs we studied, seaweeds reduce *Oculina* growth directly through competition and indirectly by forcing these corals to occur primarily in low-light habitats where seaweeds are rare (Figs. 3, 4, and 13) but where the growth of the corals is also constrained by low light (Miller 1995). Despite the consistent reduction in coral growth caused by seaweeds, we observed mean negative growth of corals transplanted into seaweed beds only at the 43-km site (Fig. 6). At the Radio Island site, coral growth under seaweed competition was reduced, but still positive (Figs. 5 and 8). If the growth rates we measured over a period of weeks are representative of longer term patterns that would occur over years, then our results do not fully explain why *Oculina arbuscula* does not form accreting reef structures at some sites in these latitudes. In fact, a congeneric species, *Oculina varicosa*, does form reef-like thickets off east Florida, but only at great depths (80 m) where light is essentially absent (Reed 1980, 1981) and seaweed competition presumably nonexistent. Had our growth experiments run longer, we might have observed more negative growth or mortality of corals at our inshore site. Alternatively, accretion of reefs may not occur because seaweeds, or associated restriction to low-light habitats, slow coral growth enough so that rates of bioerosion exceed the rates at which coral skeleton accumulates. Highsmith (1980) indicated that global patterns in coral bioerosion are correlated with productivity or nutrient concentrations. Thus, the increasing nutrient concentrations from tropical to temperate waters might increase bioerosion in temperate

locations. *Oculina arbuscula* in North Carolina is subject to infestation by a diverse cryptofauna (McCloskey 1967) including bioeroders such as boring sponges and bivalves (M.W. Miller, *personal observation*). Rates of *O. arbuscula* bioerosion have not been determined, but it is plausible that limited growth combined with high rates of bioerosion could prevent reef accretion by *O. arbuscula*. Structural weakening by intense bioerosion would also make *O. arbuscula* more susceptible to damage from physical disturbance, putting them at further disadvantage with respect to seaweeds in shallow, high-energy environments.

In addition to seaweed's effects on growth rate, seaweeds also inhibited the recruitment of *Oculina* larvae at the Radio Island site. Recruitment of coral larvae was high in deep habitats where seaweeds were absent but very low in shallow habitats dominated by seaweeds. This could have produced the pattern we noted of mature corals being more numerous at 6 m deep than at 1 m deep (Fig. 3) despite these corals being more physiologically suited to the shallower depth (Miller 1995). When seaweeds were experimentally removed from shallow areas, recruitment increased dramatically and was not significantly less than in the deep habitats (Fig. 13), though the power of this test was extremely low ( $\beta = 0.05$ ).

Despite this demonstrated suppression of coral recruitment by seaweeds, absence of larval recruitment alone is not a sufficient explanation for the rarity of *Oculina* on offshore reefs where seaweeds are abundant (Fig. 4). When we carefully examined larger areas ( $1 \times 50$  m transects) on these reefs, we almost invariably found that a few *Oculina* had colonized, but that they were  $13\times$  more numerous on the vertical sides of the ledges, where seaweeds were rare, than on immediately adjacent horizontal areas, where seaweeds were common. Additionally, when collecting seaweeds from sand plains behind the algal-dominated ledges, we commonly found a few seaweeds attached to weathered, and apparently old, *Oculina* fragments (M.E. Hay, *personal observation*), suggesting that *Oculina* may have occurred in these habitats for considerable periods of time. Dispersal of *Oculina* has thus allowed it to colonize a wide variety of inshore, nearshore, and offshore reefs, but the coral has been able to become abundant only on reefs, or in microhabitats, where seaweed cover is low.

High sedimentation on horizontal vs. vertical substrates could have contributed to the above pattern, but effects of sedimentation seem limited relative to the effects of seaweeds. We did not directly address the effects of sedimentation on *Oculina*, but when we removed seaweeds from the horizontal substrates assessed above, corals grew well whether they were on the substrate where sand-scour and sedimentation should occur or suspended above the substrate where these stresses should be minimized (Fig. 6). If the seaweed canopy was left intact, corals lost mass regardless

of their position on, or above, the substrate. Additional unquantified field observations also suggest that sedimentation is not a major deterrent to *Oculina arbuscula*. Turbidity and sedimentation at the 8-km site are potentially high as evidenced by the low visibility (often 3 m or less) and high abundance of flocculent particles that are clearly visible in the water column; however, *Oculina* is abundant at this site. In contrast, at the 43-km site, waters are clear (visibility often 20 m or more) and particulates in the water seem uncommon, yet *Oculina* is rare. These patterns occur for other reefs as well. In recent dives on seven clear-water reefs (about 43 km offshore and 27 m deep) and three turbid-water reefs (about 8–10 km offshore and 17 m deep) off North Carolina, *Oculina* was obviously more abundant at the turbid sites (M.E. Hay, *personal observation*). Additionally, sampling of horizontal vs. vertical substrates along the deep regions of Radio Island Jetty, a turbid site where seaweeds are completely absent, showed no significant difference in coral density between horizontal and vertical 0.25-m<sup>2</sup> quadrats (M.W. Miller, *personal observation*). Thus, when the likely confounding effects of seaweed cover and potential sedimentation are separated, sedimentation seems to have little effect.

#### *Effects of herbivores and nutrients*

Investigations on tropical reefs have consistently found that natural levels of grazing remove most seaweeds (reviewed by Hay 1991), thus preventing seaweeds from overgrowing established corals and interfering with recruitment and growth of juveniles (Birkeland 1977, Potts 1977, Lewis 1986, Hughes 1989, 1994). In contrast to this tropical pattern, we found that large grazers significantly enhanced seaweed biomass at the offshore sites (Fig. 7B) and that grazers at our inshore site had a profound effect on the species composition of the algal community, but had little (Fig. 9), or no, effect (Fig. 10) on total algal cover or biomass. Caging, therefore, had no significant effect on coral growth at these sites (Figs. 7A and 8), but grazing fishes did remove barnacles at the 8-km site, and this was correlated with enhanced *Oculina* recruitment (Fig. 12).

Our experiments did not explicitly distinguish effects due to fishes vs. urchins, but urchin grazing would have been low to nonexistent at our offshore sites. Urchins (*Arbacia punctulata* and *Lytechinus variegata*) were very rare at the 43-km site, and urchins (*Arbacia punctulata*) were removed from the 8-km site during 1991 and 1992 as part of another experiment (M. E. Hay, *unpublished manuscript*). Thus, our offshore experiments reflect primarily the effects of fish grazing (urchins, however, were present in the Radio Island experiments). Access by these fishes increased, rather than decreased, seaweed abundance. This apparently occurred because the common seaweeds at these sites are brown algae that are unpalatable to local fishes but

selectively eaten by certain amphipods and polychaetes (Hay et al. 1987, 1988, Duffy 1990, Duffy and Hay 1991, 1994). Omnivorous fishes consume these mesograzers and thus increase recruitment and growth of the brown seaweeds (M. E. Hay and J. E. Duffy, work in progress). In other temperate and tropical locations urchins have been shown to dramatically impact seaweeds (Lawrence 1975, Lessios 1988, Andrew 1993), and, when abundant, their feeding can prevent both temperate and tropical corals from being overgrown by seaweeds (Hughes et al. 1987, Hughes 1989, 1994, Coyer et al. 1993). However, in the tropics, caging out fishes alone can result in seaweeds overgrowing and killing corals (Lewis 1986); this was clearly not the case at our temperate sites, where excluding fishes had no strong effect on coral growth.

In contrast to our findings when we manipulated only large grazers, a factorial experiment manipulating both large grazers and nutrients demonstrated that nutrients significantly increase the cover (but not mass) of bushy red seaweeds in cages that excluded herbivores (Fig. 10), and that increases in these algae are associated with significant reductions of coral growth in full cages (Fig. 11). Though nonsignificant ( $P = 0.088$ ), there was a possible interactive effect of the nutrient and caging treatments on coral growth. We postulate that these effects are indirect (via algal competition), and so might expect them to be more difficult to document statistically. The patterns of coral growth between treatments (Fig. 11) are consistently opposite to the pattern in total seaweed cover, which does show significant interaction (Fig. 10). Also, this experiment showed a significant cage effect, while a prior caging experiment without nutrient addition did not yield a significant cage effect (Fig. 8). Taken together these patterns suggest that: (1) spread of bushy red seaweeds, but not arborescent browns, at this site is nutrient limited, (2) the palatable red seaweeds are removed so rapidly by local herbivores that their increased growth due to nutrient additions can be seen only in grazer-exclusion treatments, (3) if reds have access to increased nutrients, they suppress coral growth so long as they are not removed by herbivores, and (4) if herbivores control the red seaweeds, then *Oculina* growth appears to be facilitated, rather than suppressed, by nutrient additions (Fig. 11). Moderate nutrient pulses can also increase the growth of tropical corals, so this is not fundamentally different than patterns previously seen on tropical reefs (Meyer et al. 1983).

The above interpretation implies that red algae exert a greater competitive effect on *Oculina arbuscula* than do brown algae. This difference may be accounted for by the morphologies of the dominant species in these two groups. The most common red alga, *Hypnea musciformis*, has a branched, bushy morphology that forms compacted turfs in which diffusion gradients would be expected to limit its access to nutrients (Hay 1981). It also has branch tips that form tendrils that rapidly at-

tach to and grow around other organisms (Hay 1986). *Hypnea* is thus capable of rafting through the water column, snagging on live corals, and overgrowing them. In contrast, the most common brown alga, *Sargassum filipendula*, is arborescent, relatively tall, and attached by a single holdfast to the rock substrate. *Sargassum* flaps back and forth with surge and currents and so moves through more water and thus experiences a much greater nutrient flux than the bushy and more compacted *Hypnea*. Unlike *Hypnea*, *Sargassum* cannot adventitiously attach to other organisms. We never observed *Sargassum* growing on, or attaching to, corals. Thus, nutrient addition may inhibit coral growth in full cages if red algae (that dominate when protected from grazers) are enhanced by nutrient addition and exert a strong competitive effect on corals. In contrast, nutrient addition may not affect coral growth in open cages because brown algae are not affected by the types of nutrient addition performed in this experiment.

#### *Contrasts with tropical reef community structure and processes*

Our study of a single species of temperate coral in one geographic region will not rigorously answer broad questions about global distribution of plant- vs. animal-dominated communities. However, because this is one of the few high-latitude systems in which these questions have been addressed with a controlled, experimental approach, it may be useful to contrast our findings with those from tropical reef communities.

Grazing fishes and urchins have profound effects on benthic community structure on tropical reefs (Lessios 1988, Hay 1991, Hughes 1994). Small-scale caging experiments have resulted in explosions of seaweed biomass (Hatcher and Larkum 1983, Carpenter 1986, Lewis 1986, Morrison 1988) and declines in live coral cover (Lewis 1986). Larger-scale reductions in grazing intensity, such as the mass mortality of the herbivorous sea urchin *Diadema antillarum* throughout the Caribbean, also result in corals being suppressed by seaweeds (Hughes et al. 1987, Lessios 1988, Hughes 1989, 1994, Carpenter 1990) at reefs where *Diadema* had been abundant. This pattern contrasts with our findings in North Carolina, where herbivory increased the abundance of unpalatable brown seaweeds, and thus compensated for the loss of palatable red seaweeds. Total mass and cover of seaweeds were largely unaffected by herbivores in North Carolina; however, coral growth may have been affected by the herbivore-induced shift in the species composition of the dominant seaweeds.

This relative difference in palatability of red vs. brown algae is not a consistent pattern in the tropics; tropical herbivores seem less choosy. As an example of differential herbivory between a temperate and a tropical reef community, Hay (1984b), Lewis (1985), and Paul and Hay (1986) demonstrated that many algae, including species of *Sargassum* and *Padina*, were rapidly consumed by herbivorous fishes on coral reefs in

the Caribbean. These genera are among those that we refer to as "unpalatable browns" and they dominate (*Sargassum*) or are common (*Padina*) in our North Carolina study sites. Apparently, the modest morphological and/or chemical defenses in these seaweeds deter the omnivorous consumers present in our temperate community but do not deter tropical herbivorous fishes.

Fishes and urchins in North Carolina do not appear to consume corals directly, as evidenced by the general lack of caging effects in most of our experiments (Figs. 7 and 8) and by many hundreds of diver hours on North Carolina reefs, during which we have never observed direct consumption of corals in the field. None of our experimental transplants showed signs of predation. This also contrasts with tropical reef communities where corallivory by fishes and invertebrates or direct mortality caused by damselfishes are important forces structuring benthic communities and controlling reef development (Glynn et al. 1978, Sammarco and Williams 1982, Wellington 1982, Glynn 1985 and 1988a, Cox 1986, Littler et al. 1989, Knowlton et al. 1990, Kenchington and Kelleher 1992). At the 8-km site the data shown in Fig. 11B, and observed grazing scars on the substrate, suggest that fish do consume barnacles but not recruiting corals. Birkeland (1977) similarly observed that tropical grazing fishes in Panama avoid eating coral recruits as small as 3 mm in diameter.

Understanding that grazing and nutrient regimes may interact in affecting competitive interactions between corals and algae (Figs. 10 and 11) may provide insight into the mechanisms of tropical reef degradation evidenced by replacement of corals with seaweeds when reefs are stressed (Marszalek 1981, Smith et al. 1981, Tomascik and Sander 1987, McClanahan and Shafir 1990, Bell 1991, Done 1992, Knowlton 1992, Hughes 1994). Seaweed and coral abundance on a given reef result from a balance of forces adding to (nutrients, light, temperature) and limiting or removing (grazing, storms, competition, sedimentation) their productivity and accumulation of biomass (see Steneck and Dethier 1994). Anthropogenic disturbances rarely alter only one factor at a time, and the multifaceted effects of overfishing (Hay 1984a, Hay and Taylor 1985, McClanahan and Shafir 1990, Hughes 1994) and eutrophication (Hatcher et al. 1989) probably interact not only with each other, but also with other disturbances such as storms, El Niño events (Glynn 1988b), epidemic die-offs (e.g., *Diadema antillarum* in the Caribbean), or outbreaks of key species (e.g., crown-of-thorns starfish, *Acanthaster planci*, in Australia), yielding profound changes in coral reef communities (e.g., Hughes 1989, 1994, Knowlton 1992). We are unaware of other published experimental studies on tropical coral reefs designed to detect interactive, or synergistic, effects of environmental perturbations on both coral and algal components of benthic communities. Our results from North Carolina reefs show that effects of nutrient additions and herbivory can interact synergis-

tically to affect coral growth. Given the general paucity of nutrients and large impact of herbivores on tropical reefs, we expect that these, and other, types of synergistic effects may be even more important on tropical reefs (also see Hatcher et al. 1989, Hughes 1989, 1994, Knowlton 1992).

Our results, showing that seaweeds appear to limit *Oculina* from numerous habitats in this temperate region, are consistent with the global-scale hypothesis of Johannes et al. (1983) that latitudinal restriction of coral reefs occurs due to a shift in competitive dominance from corals to seaweeds as latitude increases. However, it can be argued that seaweeds may also be the competitive dominant in tropical coral reef communities, but that they simply get eaten so rapidly there that their competitive superiority is rarely expressed. Both manipulative experiments and natural die-offs of common herbivores on tropical reefs suggest that seaweeds do damage corals if herbivory is decreased (Lewis 1986, Hughes 1989, 1994). Other more subtle changes in factors affecting the well being of seaweeds vs. corals (nutrients, sedimentation, turbidity, etc.) could also promote replacement of corals by seaweeds, or could interact synergistically with herbivory in determining reef structure.

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